

# Polyploid evolution: Keeping the peace at genomic reunions

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**Incompatible gene or chromosomal combinations brought together in allopolyploid genomes cannot be purged through Mendelian segregation. But recent studies suggest that the elimination of DNA sequences and alteration of DNA methylation patterns may permit the restoration of fertility in some allopolyploids.**

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Evolutionary biologists mostly think about how organisms, genes and genomes diverge. Darwin initiated this trend with his account of how natural selection explained the divergence of species so that now evolutionary trees, rather than webs, are the accepted means for depicting relationships between genes, populations, species and higher taxa. However, evolution is not just about divergence. Major evolutionary transitions, such as the origins of the first cells and the first eukaryotic organisms, are thought to have been facilitated by bringing divergent genes and genomes together [1]. Similarly, the reunion of genomes through hybridization and allopolyploidy is conservatively estimated to account for 2–4% of speciation events in flowering plants and 7% in ferns [2], and most plants appear to be paleopolyploids. Given the importance and ubiquity of these genomic reunions, biologists have become increasingly interested in how genomes adjust when they come into contact with each other [3]. Two recent studies [4,5], in particular, have provided new insights into the processes that may contribute to such adjustments in allopolyploid plants.

In eukaryotes, genomic reunions usually are a consequence of sexual hybridization. In most cases, divergent genomes do not coexist peacefully upon first contact and hybrids, if formed at all, are inviable or sterile [6]. There are mechanisms, however, by which the problem of hybrid incompatibility can be circumvented. In the simplest case, selection favoring the most fertile or viable hybrids can lead to the rapid purging of incompatible gene combinations (Figure 1a) or chromosomal rearrangements that cause sterility or inviability [7]. Alternatively, the hybrid genome may be duplicated (allopolyploidy) and, if chromosomal rearrangements are the cause of hybrid incompatibilities, the new allopolyploid is likely to be fertile.

As explained more than half a century ago by Dobzhansky [8], chromosomal doubling furnishes an exact homologue

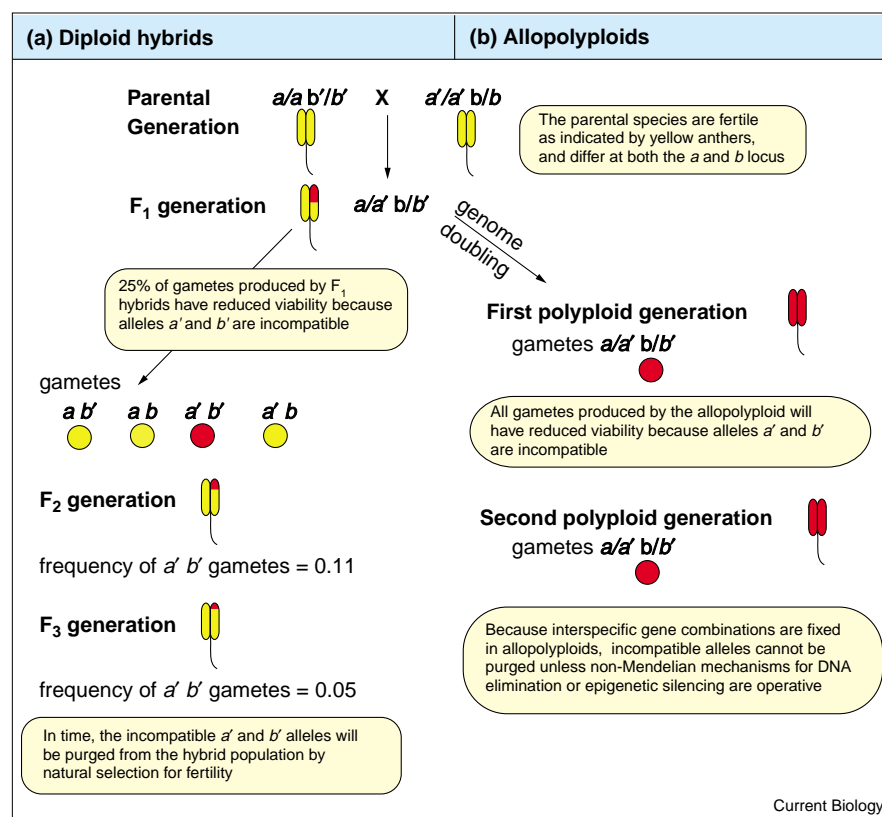
for each chromosome in the hybrid genome, thereby restoring pairing and fertility in chromosomally divergent hybrids. In contrast, chromosomal doubling should have no effect on the action of interacting genes, so sterility caused by gene interactions is preserved (Figure 1b). An exception to these two general rules is that, if the genomes combined in the allopolyploid are too similar, new meiotic problems may be created due to pairing between similar (homeologous) chromosomes from different genomes.

The two mechanisms of fertility restoration — purging versus genome doubling — have long been viewed as completely independent, because allopolyploids were considered to have fixed genomic complements with no means for purging incompatible interspecific gene combinations or chromosomal segments (Figure 1b). In fact, students of speciation have used the fertility of many allopolyploid plant species as *prima facie* evidence that most sterility in plants is caused by chromosomal rearrangements, rather than genes [6,9]. This line of reasoning may no longer be valid, however, because of recent work showing that the genomes of polyploids are flexible and dynamic, and that large-scale genomic changes may be triggered by polyploid formation.

A remarkable example of this comes from four synthetic allopolyploid lineages in *Brassica*, in which an average of 6.4% of restriction fragments differed between F<sub>2</sub> and F<sub>5</sub> plants from the same lineage [10]. Because each synthetic polyploid was completely homozygous after chromosome doubling, no changes were expected under Mendel's laws of inheritance. Unexpectedly, an independent investigation of genomic change in allopolyploid *Brassica* [11] failed to confirm the findings of the initial study, and essentially no genomic changes were found in allopolyploid cotton [12]. Thus, rapid genomic change may not be a universal consequence of polyploidy.

Perhaps the most compelling evidence for large-scale genomic changes accompanying allopolyploid formation comes from a series of papers by Moshe Feldman's lab on tetraploid and hexaploid wheat [13,14]. However, these early studies failed to compare the allopolyploids with either their parents or first generation hybrids, making it difficult to estimate the timing and rate of genomic change. Two papers published recently in *The Plant Cell* [4,5] provide this missing information and suggest a possible explanation for how divergent genomes may come to coexist peacefully in newly formed allopolyploids.

Figure 1



Fate of incompatible interspecific gene combinations in diploid hybrids (a) and allopolyploids (b). Additive gene action is assumed.

Wheats make up what is probably the world's most famous allopolyploid complex. The complex includes diploid, tetraploid and hexaploid wheat species. Hexaploid bread wheat is the most widely grown, containing three divergent genomes — AABBDD (Figure 2). However, various tetraploid wheats (AABB) are also widely grown for bread, beer and pasta. Numerous natural allopolyploid combinations have also been found, involving several different diploid and tetraploid species. Thus, the group offers an excellent system for studying the timing and repeatability of genomic changes that accompany polyploid formation.

In the first of the two new papers, Ozkan *et al.* [4] focused on the dynamics of two kinds of repetitive DNA sequences in a variety of first generation hybrids, synthetic allopolyploids and parental plants. These repetitive sequences do not include genes, but are specific to either individual chromosomes or several chromosomes of a genome and thus may play a role in the initiation of meiotic pairing. Remarkably, both chromosome- and genome-specific sequences were eliminated in a reproducible manner that was determined by the combination of genomes found in the hybrids and allopolyploids. Elimination of genomic-specific sequences was initiated in the first generation hybrids, while loss of

chromosome-specific sequences did not begin until the allopolyploid had formed. The genomic changes appeared to be largely complete by the third generation following polyploid formation, and were accompanied by an increase in seed fertility and a reduction of irregular chromosome pairing in meiosis. Both kinds of sequences were found to be more commonly lost in allopolyploid combinations that occur naturally than in combinations exclusive to the laboratory.

Ozkan *et al.* [4] interpret these data as evidence that the elimination of these two kinds of sequences likely played a critical role in polyploid establishment by restoring diploid-like behavior at meiosis [4]. This is an intriguing idea, but it is supported by correlative evidence only. An alternative explanation, put forward in an earlier paper by Feldman's group [13], is that the necessary chromosome divergence occurs through the differential loss of low-copy sequences. This latter explanation is consistent with evidence from the second paper in the pair [5], which reports that a large fraction of the genome experiences sequence elimination and that the majority of eliminated sequences are low-copy. Note that the loss of low-copy sequences must necessarily correlate with the restoration of fertility and diploid-like behavior as well.

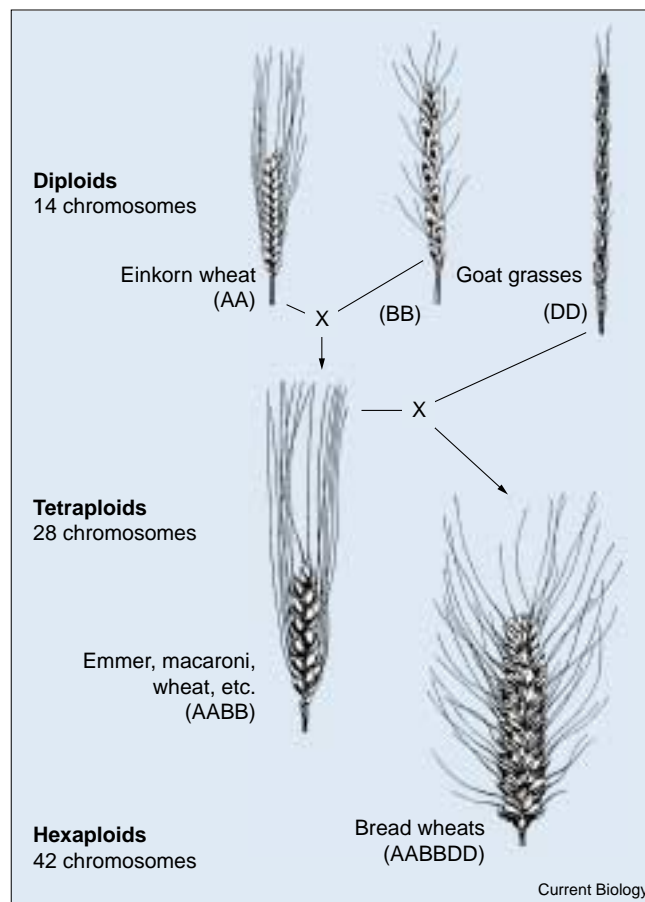
Shaked *et al.* [5] employed a somewhat different strategy to study genomic change. Rather than monitoring a small number of known sequences in many hybrid and allopolyploid combinations, they assayed many anonymous DNA sequences — sequences of unknown copy number or function — in only three combinations of parental individuals, first generation hybrids and allopolyploids. They also searched for altered patterns of DNA methylation. DNA methylation appears to have several functions in plant genomes, including the regulation of gene expression, defense against viral infection and repression of transposable elements — segments of DNA with the ability to move about the genome.

As with the repetitive sequences studied by Ozkan *et al.* [4], Shaked *et al.* [5] found that elimination of the anonymous sequences was both widespread and repeatable. Indeed, 66 of 619 (10.6%) sequences assayed were eliminated, and sequence loss was evenly divided between the first generation hybrids and allopolyploids. Further analysis of a small subset of the eliminated sequences revealed that most correspond to low-copy DNA. Substantial alterations were also observed in methylation patterns, with the majority of changes occurring in first generation hybrids (6.9%) and the minority in the allopolyploid (4.4%). Most of the methylation-altered sequences in the first generation hybrids correspond to repetitive sequences, including retrotransposons, a kind of transposable element. Note that the retrotransposon sequences were demethylated. This seems odd because retrotransposon activation should lead to an increase in genome size, rather than to sequence elimination as reported here. In allopolyploids, low-copy and repetitive sequences were found to be altered in roughly equal numbers.

So do these genomic changes facilitate the establishment of allopolyploids? Following the lead of McClintock [15], some authors have suggested that changes such as these may represent preprogrammed adaptive responses to genomic stress caused by hybridization and polyploidy, and serve to stabilize polyploid genomes. However, the situation is more complex. In particular, enhanced transposable element activity in hybrids is most likely to be maladaptive, because hybrids already suffer from too much genetic and phenotypic variability. A similar argument can be made for most other genomic changes in diploid hybrids.

The circumstances are somewhat different for allopolyploids. Unlike diploid hybrids, some incompatible gene or chromosomal combinations are fixed in allopolyploids and cannot be purged through Mendelian segregation (Figure 1b). DNA excision or methylation may thus permit their elimination or silencing. Again, it is important to note that most changes are likely to be neutral or

Figure 2



Evolution of domesticated wheats. (Modified from [16].)

maladaptive with respect to fitness. However, natural selection for viability and fertility provides an effective filter that eliminates gametes and individuals carrying maladaptive changes and favors those inheriting advantageous changes. This process may account, in part, for the repeatability of the genomic changes observed in wheat allopolyploids [4,5].

Unfortunately, the mechanism underlying the widespread excision of genomic sequences is unknown, but a number of plausible molecular mechanisms are listed by Shaked *et al.* [5]. Experiments designed to elucidate the mechanism of sequence elimination should be a primary focus of future studies of allopolyploid genome evolution. Most likely, sequence elimination results from the breakdown of some ordinary cellular function. It may happen to permit allopolyploids to respond to fertility selection, but this role is likely to be entirely fortuitous.

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